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A STUDY OF FACTORS IN THE DEVELOPMENT OF IPS OUTBREAKS IN PONDEROSA PINE

Progress Report of Southern Sierra Studies - Season of 1948

By

George R. Struble

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A STUDY OF FACTORS IN THE DEVELOPMENT OF IPS OUTBREAKS IN PONDEROSA PINE

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INTRODUCTION

Severe sporadic outbreaks of pine engraver beetles in 1944 resulted in the initiation of studies to determine the causes underlying these outbreaks. In northern California, the investigative work was started in the vicinity of Hat Creek field base during 1945; studies in the Southern Sierra Subregion were begun in 1946 in the vicinity of Miami field base. The primary purpose of this work is to secure essential information needed in the management of ponderosa pine stands to minimize or prevent outbreaks. Studies in the Hat Creek area where Ips confusus Lec. and I. oregoni (Mich.) are both active are concerned primarily with climate and ecology, while those at Miami, where I. confusus alone is active, deal with biology and host relationships.

This is the third seasonal report of studies in the Miami area. The first, in 1946,1/ presented the results of exploratory work which uncovered much information of value in interpreting the course of continuing infestations and in laying the groundwork for further studies. The 1947 report2/ presented the results of further detailed study and experimentation on seasonal biology, habits, and factors concerned in the breeding environment which limit brood success. Much was learned about natural insect enemies and host characteristics. In 1947, field tests of the influence of phloem moisture on the development and success of broods indicated that this factor was important.

Infestation conditions within the study areas in western Mariposa and Madera Counties during this period proved most favorable to detailed investigations. The beginning of aggressive outbreaks in reserve stands near logging operations was evident in the late summer of 1946. In 1947, epidemic outbreaks were found in the vicinity of nearly all logging operations and

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1/ Struble, G. R. 1947. A Study of Factors in the Development of Ips Outbreaks. Progress Report of Sierra Studies - 1946.

2/ Struble, G. R. 1949. Biological and Host Factors in Relation to Ips Outbreaks in the Southern Sierra Subregion. Progress Report - Season of 1947.

other cutting areas where there were spring and summer slash accumulations. Despite the same degree and character of slash in 1948, outbreaks were reduced almost to obscurity in the localities most heavily affected the previous year. Thus, there was presented a fluctuating cycle from which much valuable information was gained in a relatively short period of time.

This report of 1948 investigative work[3/] presents the results of further detailed data from experimentation and records of developments throughout the year and points to the need for further study. The main points considered are: (1) Seasonal influences contributing to the success or failure of broods; (2) further information on life cycle and habits in comparison with these elements in previous years of study; (3) the importance of certain biotic factors on brood production; (4) the significance of host moisture in the production of broods.

GENERAL CONDITIONS AFFECTING BREEDING IN 1948

The overwintering populations

The attacks and successful establishment of heavy early seasonal broods evidently are dependent upon the successful survival of overwintering populations in slash or in trees attacked the preceding fall. The survival of adults through the winter period 1947-1948 in the abundant late summer and fall logging slash and in the numerous infested trees attacked in the fall of 1947 appeared high enough to allow the establishment of aggressive 1948 spring broods in fresh slash. Spring emergence data from typically representative slash attacked during the late summer and fall of 1947 revealed an average number of 148 adults per square foot in nine square feet of bark area placed in emergence cages. The emergence from four representative infested tree samples (12 square feet of bark area) attacked during the fall of 1947 in the same area as the slash amounted to an average of 52 adults per square foot. Thus, while the survival of adults overwintering in slash was indicated to be about three times the number in standing trees, the overall populations available to attack early spring slash evidently were heavy and sufficiently adequate to infest all suitable slash material on the ground.

Availability of slash material

The open, dry winter period in the areas studied allowed the continuance of logging activity, and this was taken advantage of in several areas at lower elevations. One sizeable area near Oakhurst, California, for example, was logged intermittently from November 15 to February 15. The slash material created during the winter and the fresher material available after resumption of regular logging schedules in April, 1948, provided an abundance of breeding media for emerging overwintered populations. Thus was indicated a setting for another year in which possible epidemic breeding would cause severe subsequent losses in the reserve stands.

3/ Grateful acknowledgment is expressed for the capable assistance of Robert A. Corey, field aide, in the completion of this assignment.

Climatic conditions

Low temperatures, usually coupled with heavy precipitation during the spring months, greatly retarded insect activity as compared with 1947. Although attacks were observed in green slash created during the winter and spring months after April 15, they were few in number until after the first of June. As indicated from emergence data on overwintered broods, the period extended until the first week in July with the peak period about June 20. Thus, it was shown that the full development of first generation Ips broods did not occur until the latter part of June. This situation was borne out by field records of attacks in slash material. Late seasonal weather conditions, particularly lowered temperatures, evidently were responsible for retarded development and possibly for poorer broods and generally reduced populations.

Character of slash material

Except in timber sales areas of federally-owned land, all of the slash created primarily as a result of logging operations in 1948 was similar to that created in previous years. It consisted of untrimmed tops varying in maximum diameter from 14 to 24 inches (Photo. #1). As previously determined, this type of slash constitutes the principle breeding medium from which emerge large populations of progeny adults (Photo. #2). Cull logs and other larger diameter material were limited in quantity and, as in the past, were not important from the breeding standpoint.

On sales areas of government-owned land, all of the tops were trimmed immediately after felling as stipulated in the logging contract. This procedure greatly limited the breeding surface by opening the main stems of tops to the heating effects of the sun and by preventing moisture losses, thereby tending to create unsatisfactory breeding conditions.

In general, the slash created in 1948 was available in abundance and appeared fully as satisfactory for the development of sustained high populations as in previous years.

SEASONAL BIOLOGY AND HABITS

Flight, attacks, and generations

As indicated previously, the spring flight of adults emerging from slash and standing trees in which they overwintered started about April 15 and continued until the first week in July with a peak around June 20. The flight and attack by adults originating in the first generation occurred between June 20 and August 30 with a peak period between July 20 and August 5. The resultant second generation broods reached maturity and emerged to attack and establish third generation progeny between August 15 and September 30 with a peak flight period around September 10. Thus, the flight, attacks, and establishment of first generation broods were extended over a period of more than 75 days, second generation broods more than 50 days, and third generation broods more than 45 days.

The schedule of 1948 generations is as follows:

Generation	Events and Period: Date: Attacks	Events and Period: Date: Emergence	Days
I	4/15- 7/15	6/26-8/ 3	110
II	7/ 1- 8/ 1	8/15-9/16	78
III	8/ 5-10/ 1	Overwinter	

All data indicated that the third generation would overwinter beneath the bark in advanced stages of development. One less generation was established in 1948 compared with the developments as shown below for the 1946 and 1947 seasons.

Generation	Events and Period: Date: Attacks	Events and Period: Date: Emergence	Days
	1946 Broods		
I	4/15-6/ 5	6/15- 7/15	88
II	6/15-7/10	7/30- 8/30	75
III	8/ 1-8/20	9/10-11/ 1*	91
IV	9/15-Overwinter		
	1947 Broods		
I	3/15-5/15	5/15- 7/15	90
II	5/20-7/ 1	7/10- 8/ 1	71
III	7/ 5-8/ 1	8/10- 9/10*	66
IV	8/20-9/20	Overwinter	

*Part of generation III remained under bark as adults without emerging until the following spring.

Duration of brood stages

The development periods from egg through larval, pupal, and adult stages were subject to great variation, principally in the larval stage. Eggs usually were hatched within ten days after deposition. Larval periods varied from 8 weeks during the spring and early summer to 20 days during August and September. Pupal development varied from 8 to 14 days.

Abundance of broods produced

The number of adults reaching maturity and emerging to establish subsequent progeny in favored host material was greatly reduced over the previous year in all areas of slash sampled. This was true of both summer generations, and in fact, there was little difference in number--as is shown by the data in Table 1. This is in great contrast to the high population trends shown in 1946 and again in 1947.

TABLE 1.--Number of Progeny Adults Emerging From Representative Slash in 1948

Location of Slash	No. Samples	Bark Area-- Sq. Ft.	Emergence Per Sq. Ft.
	Generation I		
Comer Ranch	1	3	148
Moore Ranch	1	3	101
Green Ranch	3	9	102
McKenzie Ranch	3	9	89
Ferguson Ranch	3	9	60
Shaw Ranch	3	9	148
Totals	14	42	108 (Av.)
	Generation II		
Nordeen Ranch	3	9	162
Clarks Valley	3	9	60
Chowchilla	1	3	144
Ferguson Ranch	3	9	164
Elliott's Ranch	1	3	74
Darrah	1	3	90
Totals	12	36	116 (Av.)

A three-year comparison in development from samples of mature brood taken in the same general areas each year (Table 2) shows the decided upward population trends of 1946 and 1947, and a downward decline in 1948. The rapid change in brood production status in 1948 occurred despite indicated normal broods from a full complement of attacks and increased egg gallery length.

TABLE 2.--Comparative Ips Development in Fresh Slash, 1946-1948

Year	Samples: No.	Samples: Area-- Sq. Ft.	Attacks Per Sq. Ft.	In. Egg Gal. Per Sq. Ft.	Ips confusus Brood: Total	Ips confusus Brood: Per Sq. Ft.	Ips confusus Brood: Per In. of Egg Gal.	Ratio Progeny to Parents
1946	23	42.81	10.60	59.02	7,715	184.1	3.08	5.41
1947	21	41.50	8.60	65.70	8,220	208.0	3.11	7.56
1948	30	90.00	9.00	79.90	10,858	120.6	1.83	4.15

The greatest reduction in broods in 1948 occurred in areas where the most active aggressive killing was prevalent in 1947 even though no effort was made to control outbreaks, and the cutting of timber and subsequent slash as favorable breeding material were essentially the same. For example, in 1947 the killing in western Mariposa County in the vicinity of Jerseydale amounted to more than 3,000 merchantable-size trees and poles, and an unknown number of reproduction-size trees, in an area of less than 2,000 acres where logging was continuous throughout the summer. The same area in 1948 contained no more than a dozen trees currently attacked by late fall, and most of these were topkilled. Furthermore, there were no attacks or killing in reproduction-size trees.

Marked differences in populations of adults produced in slash during the two years, as shown by Table 3, tend to shed some light on the reasons for inactivity in reserve stands during 1948. As mentioned, similarities in slash quality, quantity, and attacks occurred during both years while there were differences in climatic conditions and, presumably, in stand vigor. Therefore, the differences exhibited in aggressiveness, in addition to lowered populations, were probably the result of greatly increased stand resistance resulting in unattractiveness to beetles. This is offered as a partial explanation for the sudden great decline in 1948. The population data presented by the table are believed to typify the numbers in the area during the two years.

TABLE 3.--Comparative Emergence from Western Mariposa County Slash in 1947 and 1948

Sample No.	Location	Bark Area-- Sq. Ft.	Period	Emergence of Ips Confusus: Number Total	Number Per Sq. Ft.
		1947 Season			
1	Oliver Creek	3	6/11-7/28	695	231
2	Mariposa G. S.	3	6/23-8/ 4	518	173
3	W. Fk. Chowchilla R.	3	6/25-8/ 4	759	253
4	Barrett Ranch	3	7/29-9/ 2	641	214
5	Ferguson Ranch	3	7/18-8/12	402	134
	Totals			3,015	201 (Av.)
		1948 Season			
1	Comer Ranch	3	6/18-8/ 4	445	148
2	Moore Ranch	3	6/23-8/ 1	305	101
3	Ferguson Ranch	6	7/11-8/10	361	60
4	Ferguson Ranch	9	8/ 9*	1,476	164
5	Carter's Mill	3	9/10-9/20	84	28
	Totals			2,671	100 (Av.)

*Data from mature brood count

BIOTIC FACTORS AND BROOD PRODUCTION

Attacks and egg galleries

The tendency toward sustained or increasing broods was evident to about the same degree in 1948 as in the two previous years, as indicated by the number of attacks and length of egg galleries. Table 2 shows that there was no significant difference in average number of attacks in any of the three years. The greatest difference in attacks between years was shown in 1948 in the spring slash attacked by overwintered adults. The average number found was slightly more than six per square foot and that for summer broods was more than twelve per square foot, whereas in previous years there was no appreciable difference in attack intensity throughout the season. However, the ultimate brood production for 1948 was similar in both spring and summer slash, and as indicated before, was greatly reduced over previous years.

Number of parent adults

The average number of parent adults per square foot of bark area was 20 in 18 samples aggregating 54 square feet of infested spring slash, 60 in 23 samples aggregating 69 square feet of summer slash, and 63 in 8 samples aggregating 24 square feet from attacked trees in late summer. Thus, it was shown that the number of adults attacking summer slash during 1948 was three times the number attacking in the spring months. This fact indicates either a high degree of mortality among the overwintering population or heavy losses among emerged adults before they had a chance to attack slash during the prolonged cold spring. The latter possibility is strongly indicated by the survival of large numbers of mature broods of adults emerging from slash during the spring months.

The over-all populations overwintering may have been smaller than is apparent from samples, as indicated from the relatively low number of adults emerging from overwintering infested trees. Hence, it cannot be determined for certain whether there were actually fewer adults to infest 1948 spring slash or whether weather conditions were a factor limiting the ability of emerging adults to reach host material. Those which became established, however, produced broods equivalent in number per unit of infested area to those established later by their progeny.

Ratio of progeny to parents

In Table 4 which follows, data are presented which indicate the marked difference in ratio between progeny and parents in spring and summer generations during 1948. It demonstrates a tendency during the early part of the season to increase rapidly in numbers in an apparent effort to make up for winter losses.

TABLE 4.--Ratio of Progeny to Parents in Spring and Summer Broods

Brood	Samples	Area-- Sq. Ft.	Number of Adults Per Sq. Ft.				Ratio
			Parents		Progeny		
			Ave.	Range	Ave.	Range	
Spring	18	54	20	7-37	113.0	47-266	7.4
Summer	22	70	61	18-125	103.5	29-239	2.3

over

As shown by this table, the progeny of the spring generation were five times the average number of parents, while the progeny of summer broods were less than twice the average attacking number. This condition appears to result from a tendency toward overconcentration of parents in the summer generations. The average emergence of spring broods amounted to 113.0 per square

foot of infested bark area while the average number of parents was only 20, whereas the average emergence of summer broods was 103.5 while the average number of parents was 61. Thus, the ratio of progeny to parents among spring broods was over three times that among summer broods, indicating a suicidal tendency among the summer generation broods. Variations in individual samples are shown in Table 4A.

TABLE 4A.--Progeny-Parent Ratios Among Separate Samples of Spring and Summer Broods

Spring Broods			Summer Broods		
No. of Adults/Sq. Ft.			No. of Adults/Sq. Ft.		
Parents	Progeny	Ratio	Parents	Progeny	Ratio
7	47	6.8	18	89	4.9
7	105	15.0	19	57	3.0
9	150	16.4	22	98	4.4
9	53	5.9	32	239	7.5
11	101	9.2	32	210	6.6
11	92	8.1	35	71	2.0
13	259	19.9	37	133	3.6
14	82	6.0	40	29	0.7
17	111	6.6	61	78	1.3
18	102	5.8	61	157	2.5
18	66	3.5	68	137	2.0
24	168	6.9	69	41	0.6
25	215	8.6	73	57	0.8
30	41	1.4	73	78	1.1
34	208	6.1	75	89	1.2
34	113	3.3	77	104	1.3
36	42	1.2	78	138	1.8
37	79	2.2	79	126	1.6
			81	104	1.3
			81	62	0.8
			111	59	0.5
			125	122	0.9
Averages: 19.6	113	7.4	60.4	103.5	2.3

Insect enemies and associates

With three years of records as a basis, we are now in a better position to evaluate the relative importance of predators, parasites, and associated fauna but still lack the conclusiveness that can be supplied by a much longer term of records. These records indicate no correlation with the production of mature Ips broods either by separate species or by the combined species of parasites, predators, and associated fauna. Variations in number between years among the different species indicate considerable fluctuation, but this

has not caused any noticeable fluctuation of Ips populations. It has been noted that conditions of slash material which foster high Ips brood production also may foster a high population of natural enemies and associated insects, but there appears to be no great degree of consistency to indicate a trend. This is graphically presented by Figure 1 of the 1948 record from infested slash.

The distribution and occurrence of insect enemies and associates, as presented in Table 5, show that only a few species comprise the greatest number. Among the most numerous in 1948 were the colydiids, Aulonium longum and Lasconotus laqueatus; the tenebrionid, Hypophloeus sp.; the staphylinid, Phloeonomus sp.; and the cerambycid, Graphisurus sp. Those occurring most frequently included Graphisurus sp., Hypophloeus sp., the various species of Hymenoptera, Lasconotus, Aulonium, Temnochila virescens, Phloeonomus, and Thanasimus lecontei.

A comparative study of the distribution and abundance of the insect enemies occurring most frequently during the three-year period from 1946 through 1948 revealed considerable fluctuation, but this did not appear to relate to Ips brood production. As is shown by Table 6, the occurrence and total number of all species was upward in 1946, downward in 1947, and increased again in 1948 to the highest point for the three-year period. This trend was followed by all except the Hymenoptera which peaked in 1947, and Lasconotus which increased to a peak in 1948.

TABLE 6.--Relative Abundance and Distribution of Insect Enemies--1946 to 1948

Genus and Species	Percent Occurrence			Percent of Total Number Collected		
	1946	1947	1948	1946	1947	1948
HYMENOPTERA:						
All species	30	69.0	82	9	62.0	11.5
COLEOPTERA:						
Thanasimus lecontei	53	19.0	55	16	1.0	5.4
Aulonium longum	37	81.2	75	22	9.5	14.9
Lasconotus laqueatus	17	62.5	77	3	13.4	38.8
Phloeonomus sp.	20	12.5	67	6	0.6	10.3
Temnochila virescens	43	6.2	68	6	0.2	4.0
Platysoma punctigerum	13	18.7	47	3	0.6	1.1
Plegaderus nitidus	17	6.2	37	2	0.2	2.4
DIPTERA:						
Medetera aldrichii	40	31.2	52	25	9.0	6.9
Lonchaea sp.	5	31.2	38	5	1.9	1.8
HEMIPTERA:						
Anthocoridae sp.	10	25.0	48	3	1.4	2.7
				100	100.0	100.0

TABLE 5.--Insect Enemies and Associates of 1948 Ips Broods

(60 samples; 180 square feet of bark area)
(Ips adults: Total--17,424; per square foot--96.8)

Order	Family	Genus and Species	No.	% all Spp.	Occurrence: Cases	Occurrence: %
		PARASITES				
Hymenoptera		All species 1/	484	6.4	49	82
		PREDATORS				
Coleoptera	Cleridae	Thanasimus lecontei	226	3.0	33	55
	Colydiidae	Aulonium longum	625	8.4	45	75
		Lasconotus laqueatus	1,630	22.1	46	77
	Staphylinidae	Phloeonomus sp.	433	5.8	40	67
		Nudobius pugetanus	8	0.1	6	10
	Ostomatidae	Temnochila virescens	168	2.2	41	68
	Histeridae	Platysoma punctigerum	47	1.4	28	47
		Plegaderus nitidus	102	1.3	22	37
	Othniidae	Othnius sp.	1	0.0	1	1
Diptera	Dolichopodidae	Medetera aldrichii	288	3.9	32	52
	Lonchaeidae	Lonchaea sp.	76	1.0	24	38
Hemiptera	Anthocoridae	Undetermined species	113	1.5	29	48
		ASSOCIATES				
Coleoptera	Scolytidae	Ips sp.	14	0.2	7	12
		Dendroctonus brevicomis	149	2.0	5	8
		Pityophthorus sp.	74	1.0	10	17
		Trypodendron sp.	4	0.0	3	5
		Hylurgops sp.	2	0.0	1	1
		Hylastes sp.	1	0.0	1	1
	Tenebrionidae	Hypophloeus sp.	1,826	24.7	53	88
	Cerambycidae	Graphisurus sp.	672	9.1	53	88
	Buprestidae	Melanophila sp.	17	0.2	7	12
	Curculionidae	Cossonos sp.	9	0.4	30	15
Diptera		All species 2/	313	4.2	23	38

1/ Hymenoptera: Principal species are Pachyceras ecceptogastri Ratz., Pteromalidae; Eurytoma sp., Eurytomidae. Other species include Coeloides brunneri Vier., Atanycolus anocomidis Cush., Braconidae; Cecidostiba burkei Cwfd., Pteromalidae; Copidosoma sp., Encyrtidae.

2/ Diptera: Associated species, mostly midges, belonging to Sciaridae, genus Sciara; some stratiomiids belonging to genus Neopachygaster.

These fluctuations occurred without any indicated evidence of influence by Ips brood abundance. In 1947, as previously shown, the production of Ips broods reached a peak; however, despite this fact and the relatively abundant populations of enemies in 1946, there was a decline. The increase of enemies in 1948 occurred apparently independent of declining Ips populations. These inconsistencies cannot be explained without further detailed studies of separate species, but the general behavior indicates a relative lack of dependence of the enemies on Ips confusus. Therefore, it can be concluded from the studies thus far that little can be expected from natural enemies in regulating the epidemiology of Ips confusus. They appear to be minor compared to some of the ecological factors, and for this reason, it seems unnecessary from the standpoint of control economy to further consider their possibilities.

Among the associated insect species, cerambycid larvae were the only ones with indicated tendencies to control, but only in a very small percentage of cases (Photo. #3). The occurrence of cerambycid larvae among 1948 broods was 88 percent, as shown by Table 5. Their number per sample unit of mature Ips broods and very young stages indicated relative insignificance as a control factor. Among 60 samples representing 180 square feet of infested bark area, only seven contained sufficient numbers of small cerambycids to indicate a small degree of control through competition for food or accidental killing of Ips broods. In these samples, unusually moist conditions of phloem prevailed.

Fungi

The relative importance of fungi, particularly Penicillium sp., as a controlling agency still is largely speculative. In 1946, and again in 1947, Penicillium was cited as responsible for about ten percent of the brood failures among all recorded cases. In 1948 it was present in sufficient amount to be cited as a cause of brood reduction in about 35 percent of the recorded cases. Thus, it is indicated that this fungus can be an important factor influencing the epidemiology of Ips confusus--not by directly attacking the insect, but by contamination of the food supply. The occurrence of Penicillium is apparently dependent on certain ecological or host conditions fostering its development, and for this reason, the controlling effect is subject to considerable variability. It was evident in 1948 that conditions which fostered increased contamination were present.

HOST MOISTURE AND BROOD PRODUCTION

Significance of phloem moisture

Early in these studies phloem moisture was indicated to have an important bearing on the success of Ips confusus broods during development. The studies in 1946[1] led to the belief that "the moisture required for an adequate environment of developing Ips broods is quite exacting, deviations from which are evidently detrimental if deficient or excessive." This view was opposed to that found by Beal in 1931[4] with respect to the moisture requirements of Ips oregoni.

4/ Beal, J. A. 1931. Further studies on insects in logging operations in western yellow pine. (Unpublished report).

He found that "In slash and logs of all sizes, from one inch diameter to 3 feet, Ips oregoni have produced heavy broods under moisture conditions from 50 percent or less up to 400 percent." In view of this, there was indicated a decided difference between species as to their requirements even though the two insects are quite similar. It was reasoned that if the phloem moisture requirements of Ips confusus are quite exacting and this factor can be controlled in slash, then control of this insect may be simplified.

Tests to determine the importance of phloem moisture as related to the success of Ips confusus broods were planned for the 1947 field season. At first, currently felled trees in a logging operation were utilized, but later, test trees were selected and felled under more controlled conditions than were possible under normal logging conditions. The results of these tests[2] were not conclusive although moisture was indicated as a factor affecting the ultimate success of mature broods. Certain inconsistencies were indicated, however, which showed a need for test replications and closer control in eliminating certain variables. In general, it was indicated that excessive phloem moisture was influential in limiting the maturity of broods.

1. Procedure in 1948 test

The field test plan for 1948 was similar in many respects to that undertaken in 1947. As with the earlier test, the trees were selected in areas representing ponderosa pine sites I and II; the former was in a flat in the bottom of a creek basin, the latter on an east exposure near the top of a ridge. Both sites, located in the Hugh Ryan area and drained by Miami Creek, were within two miles of each other and differed 500 feet in elevation.

The testing procedure was similar at each location. Three pairs of trees were selected, each having similar crown, diameter, and bark characteristics. The pairs were numbered serially as 1A, 1B, 2A, 2B, 3A, and 3B. All limbs were left on the "A" series and lopped from the "B" series. All trees were bucked at 25 and 50 feet from the top immediately after felling, thus assuring the same character of breeding material as provided in a logging operation. With mid-bole sections severed, it was possible to compare the moisture conditions, attacks, and success of brood with these elements in the top sections. The general canopy of moderately-stocked ponderosa pine stands at both sites made it possible for all trees to be felled in partial or full shade during the day. Thus, the attacks to be made were in no way influenced by excessive heating by the sun.

Phloem moisture samples were taken every ten days beginning at the time of felling and continuing through the development of Ips broods to maturity. In all, five samplings were included in an elapsed time of 40 days. All samples were taken by means of an arch-punch driven through the corky outer bark into the sapwood to include ½-inch of sapwood (Photo. #4). This resulted in a cylindrical disc with a diameter slightly larger than one inch. Each disc as obtained was labelled and wrapped in aluminum foil then placed in a tightly covered metal can to prevent moisture losses through evaporation. The complete sample in a given location included three discs--one taken from the top and one from each side of the log. Each unit was handled separately. Phloem moisture determinations for a given location were based on the average

of three-disc units. Determinations of phloem and sapwood moisture from each unit were made in the laboratory through separating these elements and weighing each individually. Samples were taken from top and mid-bole sections of each tree at approximately 25 and 50 feet from the top, respectively. Weights of wet and dry samples were secured by means of a torsion precision balance. Samples were dried in an electric drying oven at a temperature of 100°C. for a period of not less than six hours.

Actual felling of test trees in both site locations was done on July 6 (Site II) and July 7 and 8 (Site I). Tree descriptions, moisture samples, bucking, and limbing of "B" trees were undertaken immediately after felling in every case. Records of attacks and brood development were taken each ten days when phloem moisture samples also were secured. With the development of Ips broods to maturity, log sections containing three square feet of bark area were cut from the top portions of each tree and placed in emergence cages. Lack of emergence cages prevented the same procedure with mid-bole sections, but data were secured through counts of mature broods in representative sections containing three square feet of bark area.

2. Description of test trees

The size of all trees under both sites is listed as follows:

Tree #	DBH	Total Height (Feet)
	Site II	
1A	16	75
1B	18	78
2A	14	82
2B	16	86
3A	14	84
3B	16	88
	Site I	
1A	20	100
1B	18	107
2A	16	90
2B	16	101
3A	16	100
3B	16	99

Bark and phloem characteristics in top and mid-bole portions of each tree were quite similar among all trees on both sites. Generally, the bark of Site I trees was somewhat thinner and the phloem somewhat thicker than these elements on Site II trees. The bark of Site II trees varied from 1/8 to 1/4 inch in thickness and the phloem 1/8 to 3/32 inch in thickness; the bark of Site I trees varied from 1/16 to 3/16 inch, and phloem from 1/8 to 7/32 inch. Mid-bole bark was slightly thicker than top bark, but no noteworthy differences

were evident in the thickness of phloem. Thus, all of the fresh material created as a result of felling these trees appeared quite similar in physical character and proved ideal in attracting Ips attacks.

3. Relation to attacks

Test trees 1A (unlopped) and 2B (lopped) from Site I were used in a series of moisture measurements to determine: (a) The adequacy of sampling as a means of obtaining reliable data because of variations in phloem moisture of test trees; and (b) the influence of moisture in limiting attacks along the bole. The phloem samples were taken after a full complement of attacks had been made. They were taken: (1) From top-bole sections fully attacked, (15 per square foot of bark area); and (2) from mid-bole unattacked sections. Differences in attack tendencies were presumed to be influenced by moisture. At each location, six or seven discs were taken from the top and sides of every log to obtain a total of 18 samples (tree 1A) and 21 samples (tree 2B). The phloem from each disc was weighed and dried individually. Table 7 presents the average phloem moisture percentages and standard deviation for the sections tested.

TABLE 7.--Average Phloem Moisture and Standard Deviation in Top (Attacked) and Mid- (Unattacked) Sections of Test Trees 1A and 2B--Site I

	Moisture Expressed As Percent of Dry Weight			
	Top Section		Mid-bole Section	
Tree No.	Average	SD	Average	SD
1A	142.8	12.5	187.8	32.3
2B	209.0	18.2	209.0	19.0

These results show that the number of samples taken was sufficient to justify conclusions on the influence of moisture on attack except, possibly, in the case of mid-bole phloem of tree 1A where the standard error was slightly more than eight percent. It was shown, therefore, that phloem moisture differences between top and mid-bole sections of tree 1A were insufficient to indicate that phloem moisture was a factor in limiting attacks. No difference whatever was found in phloem moisture between top and mid-bole sections of tree 2B.

4. Relation to brood production

The use of three discs to a given sampling in top and mid-bole sections of all trees throughout the test left considerable room for error as shown by the above standard deviation from 18 discs. However, the data are believed to show an indication sufficiently consistent to be of value in the interpretation of results and in basing tentative conclusions. Table 8 presents the phloem moisture percentages of the top and mid-bole sections of the paired trees at the beginning and ending periods of the tests in relation to Ips development for the two sites.

TABLE 8.--Initial and Final Phloem Moisture Percentages and Ips Brood Development in Lopped and Unlopped Trees--Sites I and II

Tree No.	Phloem Moisture (%) Begin	End	Gain or Loss	Ips Attacks and Emergence/Sq. Ft. Attacks	Parents	Progeny**
Site II--Top						
1A	156.5	116.1	-40.4	19	111	59
1B	170.2	239.9	+69.7	14	67	136
2A	123.0	101.2	-21.8	10	61	157
2B	151.0	234.1	+83.1	16	80	104
3A	174.0	142.4	-31.6	17	78	138
3B	138.1	184.5	+46.4	9	40	29
Average				14	73	104
Site II--Mid-bole						
1A	159.8	205.5	+ 45.7	*	*	69
1B	142.0	247.6	+105.6	*	*	86
2A	140.5	262.1	+121.6	*	66	63
2B	166.8	284.8	+119.1	*	100	49
3A	122.2	241.3	+119.1	*	*	19
3B	169.4	269.9	+100.5	15	*	39
Average						54
Site I--Top						
1A	155.3	81.4	- 73.9	17	73	78
1B	165.9	209.2	+ 43.3	14	73	56
2A	170.2	125.3	- 44.9	16	81	62
2B	158.0	219.4	+ 61.4	14	61	78
3A	161.6	143.8	- 17.5	19	125	122
3B	153.5	217.5	+ 64.0	14	69	41
Average				16	80	72.4
Site I--Mid-bole						
1A	164.4	158.7	- 5.7	*	*	126
1B	168.9	236.7	+ 67.8	10	*	35
2A	164.1	199.2	+ 35.1	*	*	63
2B	174.1	331.0	+156.9	*	*	20
3A	157.2	168.2	+ 11.0	13	*	22
3B	182.6	241.6	+ 59.0	*	*	43
Average						51.5

* Attack and parent adult counts in most of mid-bole sections were not made because of close similarity in number to top sections.

**Progeny data of top sections secured through emergence of adults, of mid-bole through count of mature broods.

The following significant points are brought out by these data: (1) The initial phloem moisture in all trees was similar, with variations from 153 to 184 percent; (2) among the 12 trees, 5, or 42 percent of them, contained higher initial phloem moisture in the top than in the mid-bole sections; (3) the phloem moisture in top sections from both sites decreased in the unlopped "A" trees and increased in the lopped "B" trees during the test period; (4) except in one case, the phloem moisture of mid-bole sections increased during the test period in both lopped and unlopped trees; (5) differences in phloem moisture did not influence attacks by Ips adults; (6) differences in phloem moisture showed no significant relation to the number of Ips broods reaching maturity in lopped and unlopped tops or in mid-bole sections; (7) lesser broods in mid-bole sections were not related to differences in phloem moisture; and (8) differences in brood production between Sites I and II were not related to phloem moisture.

These points are further illustrated by line graphs (Figures 2 and 3) which show the phloem moisture trend in top sections at ten-day intervals on the two sites. In all unlopped "A" trees, the moisture trend is downward; in the lopped "B" trees, the trend is upward. Emergence data indicated on the graphs show no correlation of moisture trend with the number of beetles emerged.

These data serve to present conclusive evidence that phloem moisture is not a reliable indication of the success of Ips brood production through maturity and does not influence attacks though earlier observations indicated that brood failures were due to excessive moisture. This does not mean that phloem moisture may not be an important factor, but measurements do not show it. It is indicated, therefore, that moisture may be closely tied in with biochemical or nutritional factors which are influential in determining brood success.

Significance of sapwood moisture

Separate sapwood moisture measurements in all disc samples revealed no indicated correlations with brood development. In all except one tree of the Site II group, the moisture trend was downward for the 40-day period of the test; the trend was downward in all trees of the Site I group. Sudden sapwood moisture declines were found in most of the trees after 30 days. The degree of decline or increase as noted for tree 1B (Figure 4) in no way was indicated to have influenced the production of mature Ips broods. It is concluded, therefore, that sapwood moisture in the ranges and gradient shown by these tests was of no significance as a factor influencing brood development.

Seasonal changes of phloem moisture in living trees

The repeated occurrence of Ips attacks in living trees of the reserve stands in late summer and fall of certain years has led to the assumption that this may be due to: (1) Lessening amounts of phloem moisture during the drier fall period; and (2) drought conditions which resulted in critical late summer deficiencies in these years.

The first point was tested in 1948 in two five-tree groups of vigorous second-growth trees 10 to 14 inches DBH. Group "A" was located on a dry south slope near a ridge-top (Site II) immediately north of Mariposa Guard Station. Group "B" was located near the bottom of a moist east slope (Site II) in the Snow Creek drainage basin one mile southwest of Mariposa Guard Station.

The testing was done by securing phloem moisture data each 30 days for a 90-day period, from June 26 to September 1. The data were taken in the same manner as previously described, i.e., by cutting discs with an arch-punch. A given sample included five discs from the upper bole (diameter six to eight inches). The phloem moisture data from these trees are presented in Table 9.

TABLE 9.--Seasonal Variation in Phloem Moisture from Upper Bole of Living Trees--1948

Tree No.	Percent Phloem Moisture			Gain or Loss--Percent
	June 24	July 28	Sept. 1	
	SITE II--DRY			
	Group A, Mariposa Guard Station			
1	140.0	155.1	168.2	+28.2
2	145.0	169.1	165.9	+20.9
3	140.8	186.9	173.2	+32.4
4	203.0	196.2	194.8	- 8.2
5	159.8	208.5	218.0	+58.2
	SITE II--MOIST			
	Group B, Snow Creek Basin			
1	233.0	197.7	184.1	-48.9
2	217.0	189.5	177.6	-39.4
3	230.5	186.1	179.4	-51.1
4	207.4	202.1	195.2	-12.2
5	194.1	195.2	189.0	- 5.1

This information revealed that : (1) With one exception, among the trees in the dry location, the phloem moisture increased with the progress of the season; (2) among the trees in the moist location, the phloem moisture consistently decreased with seasonal progress; and (3) the decrease found in phloem moisture was slight and insufficient to indicate a critical change in conditions. The surprising feature of these data is the increase in phloem moisture in the trees of the dry location; no explanation is offered. Vigor, as indicated by growth rate, was greater in the moist Snow Creek area.

It is to be noted that severe subsequent killing occurred in these same areas in 1947, but there was no killing here in 1948 even though slash conditions and breeding were similar both years. This indicates that possible critical moisture conditions may have been influential in the 1947 attacks. Further data on seasonal phloem moisture changes may throw more light on the causes of attacks in living trees.

FURTHER INVESTIGATIVE WORK NEEDED

Much additional information is needed to provide an adequate basis for controlling or preventing future outbreaks. Facts uncovered thus far indicate that there still are many elements in the biological and host association that limit the success of broods. Some which appear to affect epidemiology are: (1) The survival of overwintering populations through emergence and establishment of progeny in the spring; (2) amount and character of food supply in the form of fresh slash during the spring and summer periods; (3) biological factors in the cycle of development which limit production of successful broods; (4) climatic conditions affecting the host trees favorably or adversely; (5) climatic conditions limiting the survival of overwintering populations; and (6) climatic conditions limiting the production of seasonal broods through spring and summer. While we have information on nearly all of these elements in studies made thus far, it is much too limited on which to base conclusions. Those which are to be considered in the planning for 1949 studies are discussed briefly below.

Overwinter carry-over

Conditions conducive to a successful carry-over of overwintering broods are believed very important to the continuance of an infestation. Evidence from limited data indicates that normal winter mortality is quite high, but the degree appears to be associated with the stages that were forced into dormancy by late fall temperatures. The winter period seems to be passed most successfully in the adult stage; broods in the larval stage apparently suffer very high winter mortality, pupae to a lesser extent. Full knowledge of brood conditions at the time the weather forces dormancy evidently is an essential element in determining control needs. Therefore, studies of this phase of Ips epidemiology will receive high ranking in the 1949 field study plans.

Amount and quality of slash

Other factors being equal, the amount and quality of fresh slash in the spring and early summer periods determine largely the degree and character of late summer and fall outbreaks in reserve stands. Large quantities of slash, if poor in nutritional elements, may not be considered hazardous; but if highly nutritious, they may be very hazardous. Therefore, appraisals to determine the status of an area of slash should consider quality first. Elements in judging quality are in need of further study; those to be considered in the 1949 plans include phloem thickness and site association. Evidence resulting from studies to date indicates that high site quality produces slash unfavorable to good brood production.

Parent adult overconcentrations

Limitations on the success of broods may be the result of inherent tendencies toward overcrowding, particularly by adults during the progress of a season from spring to fall. Evidence from studies concluded indicates that overconcentrations of attacking adults occur in mid- and late summer. Additional information is needed as to whether this habit is regular each year, or whether it occurs occasionally, in determining the course of outbreaks. This element will be investigated further in 1949.

Climatic conditions

Climatic conditions affecting host trees, degree of slash deterioration, and broods directly are believed fundamental in limiting the success of broods and subsequent outbreaks. Observational evidence indicates that excessive winter moisture from rain and snow adversely affects overwintering broods, particularly the immature stages. Prolonged cold temperatures in the spring and early summer appear to greatly limit brood success by prolonging the attack and development periods, and by fostering conditions in the slash material which are unfavorable to brood production. Increased precipitation, particularly during the early growing season, is conducive to improvement in host vigor and resistance. Full knowledge of climatic factors as they affect breeding conditions and host resistance is essential in determining the course of outbreaks. Studies of climatic factors--temperature, humidity, precipitation--applicable to the southern Sierra areas will be undertaken in 1949.

SUMMARY

Seasonal investigative work was continued during 1948 on the biology and habits of Ips confusus, and on some of the biological and host factors affecting the control of this species. Previous studies in 1946 and 1947 in the Southern Sierra Subregion indicated that adequate information on these elements was basic to determining the epidemiology of this insect. Most important of these elements appeared to relate to: (1) Biological control by insect enemies, fungi, or inherent control tendencies; (2) conditions within the host forstering or inhibiting brood development, particularly phloem moisture; (3) climatic conditions of temperature and precipitation affecting development. Emphasis was placed on the biological and host factors in this season of investigation which was undertaken in the lower elevation ponderosa pine areas of western Mariposa and Madera Counties with activities centered at Miami Field Base.

Listed below are the most significant points resulting from the 1948 studies:

1. The overwinter (1947-1948) carry-over of Ips populations, primarily as adults, amounting to 148 per square foot in sampled slash and 52 per square foot of infested area in sampled trees, indicated the possibility of continued aggressive populations during 1948 in abundant slash of continuing logging operations.

2. Late seasonal rains and continued subnormal temperatures in late spring retarded emergence and inhibited the development of 1948 broods. Peak emergence of overwintering populations occurred about June 20, nearly six weeks later than in the two previous years. This resulted in one less generation, with only three completed during the 1948 season compared to four generations in each of the two previous years.

3. Mature broods produced in 1948 were greatly reduced compared with those of the two previous years. Emergence per square foot from representative samples of infested slash amounted to 184 in 1946, 201 in 1947, and 100 in 1948. The ratio of progeny to parents was 5.41 in 1946, 7.56 in 1947, and 4.15 in 1948.

4. Self-destructive tendencies were indicated by parent adult over-concentrations during summer in slash and attacked trees. Progeny-parent ratios were 6.3 in spring slash with less than 33 parents per square foot, 1.1 in summer slash with more than 66 parents, and 0.8 in summer slash with more than 100 parents per square foot. 54 percent of the samples, representing summer broods, contained over 66 parents per square foot.

5. Three years of records on the effectiveness of insect enemies and associates as controlling agents revealed: (a) No relationship between the number of single or combined species and amount of Ips brood produced; (b) occasional slight control by associated cerambycid larvae; (c) tendency toward increase of enemies and associates under conditions favorable to the increase of Ips confusus. Therefore, from the standpoint of control economy, it no longer appears necessary to consider the possibility of insect enemies.

6. Blue-green fungus, Penicillium sp., was cited as responsible for brood failures in 10 percent of recorded cases in 1946 and 1947, and in 35 percent in 1948. Its action is through contamination of food supply. Occurrence apparently is dependent on certain ecological or host conditions which foster development.

7. Detailed studies of moisture in the Ips breeding environment revealed that: (a) Phloem moisture per se was not a factor in determining or limiting attacks along a log; (b) there is considerable variation in phloem moisture in any given portion of a log; (c) attacks were uniform in top and mid-portions of all logs tested regardless of phloem moisture variation; (d) the number of successful broods produced to maturity did not relate to amount of phloem moisture; (e) phloem moisture increased during the 40-day period of study in lopped tops and decreased in unlopped tops, but the broods produced did not relate to differences in phloem moisture; (f) sapwood moisture bore no significant relation to brood production; (g) these results indicate that other factors may be more important in determining attacks and successful brood development.

8. Measurements of phloem moisture in the upper bole of living trees every 30 days during the dry summer season revealed that: (a) Among five trees on an apparently dry location, the phloem moisture increased with seasonal progress; (b) among five trees in an apparently moist location, the phloem moisture decreased with seasonal advance; (c) decreases in phloem moisture as shown were insufficient to indicate critical conditions favoring late seasonal attacks by Ips.

PHOTO. #1

Slash area on the Dr. Nordeen Ranch. Unlopped tops, varying in diameter from 14 to 24 inches at base, provided ideal breeding conditions for Ips in 1948. Average emergence from 9 square feet of infested bark area from this slash was 162 beetles per square foot. (See Page 3). (#13355)

Section of bark removed from infested slash exposing inner surface which is engraved by numerous egg tunnels and adult feeding tunnels. Close examination under slight magnification will reveal numbers of larvae, pupae, and adults of Ips confusus Lec. (See Page 3). (#13356)

PHOTO. #2

Log sections with bark removed to expose typical Ips engravings (left and center logs) and occasional heavy subsequent cerambycid (Graphisurus sp.) work (right log) on sapwood surfaces. Cerambycid larvae cause accidental mortality to a small percentage of Ips broods by feeding and destroying food supply. (See page 12). (#13357)

PHOTO. #3

PHOTO. #4

Phloem samples for moisture determinations were obtained by means of an arch punch which was driven through bark to sapwood to include $\frac{1}{2}$ inch of sapwood. This resulted in a cylindrical disc with a diameter slightly larger than 1 inch. (See page 13). (#13358)

FIGURE 1
DISTRIBUTION OF TOTAL IPS BROODS, INSECT ENEMIES, AND ASSOCIATED INSECT SPECIES IN SEPARATE SLASH SAMPLES, EACH WITH 3 SQUARE FEET OF BARK AREA

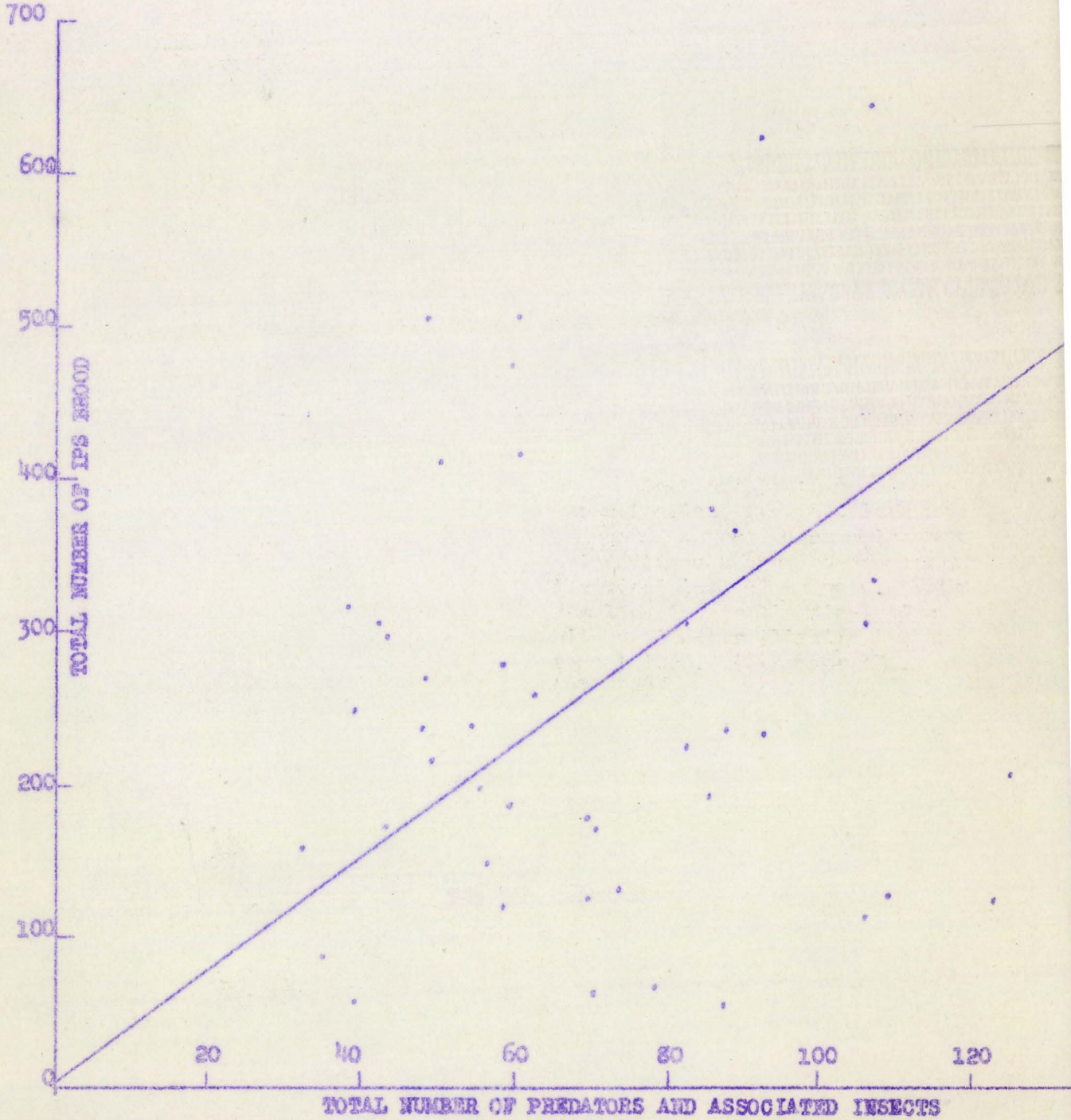

FIGURE 12
PHLOEM MOISTURE TRENDS, SITE II IN
UNLOPPED AND LOPPED TREES
_____UNLOPPED
- - - - LOPPED

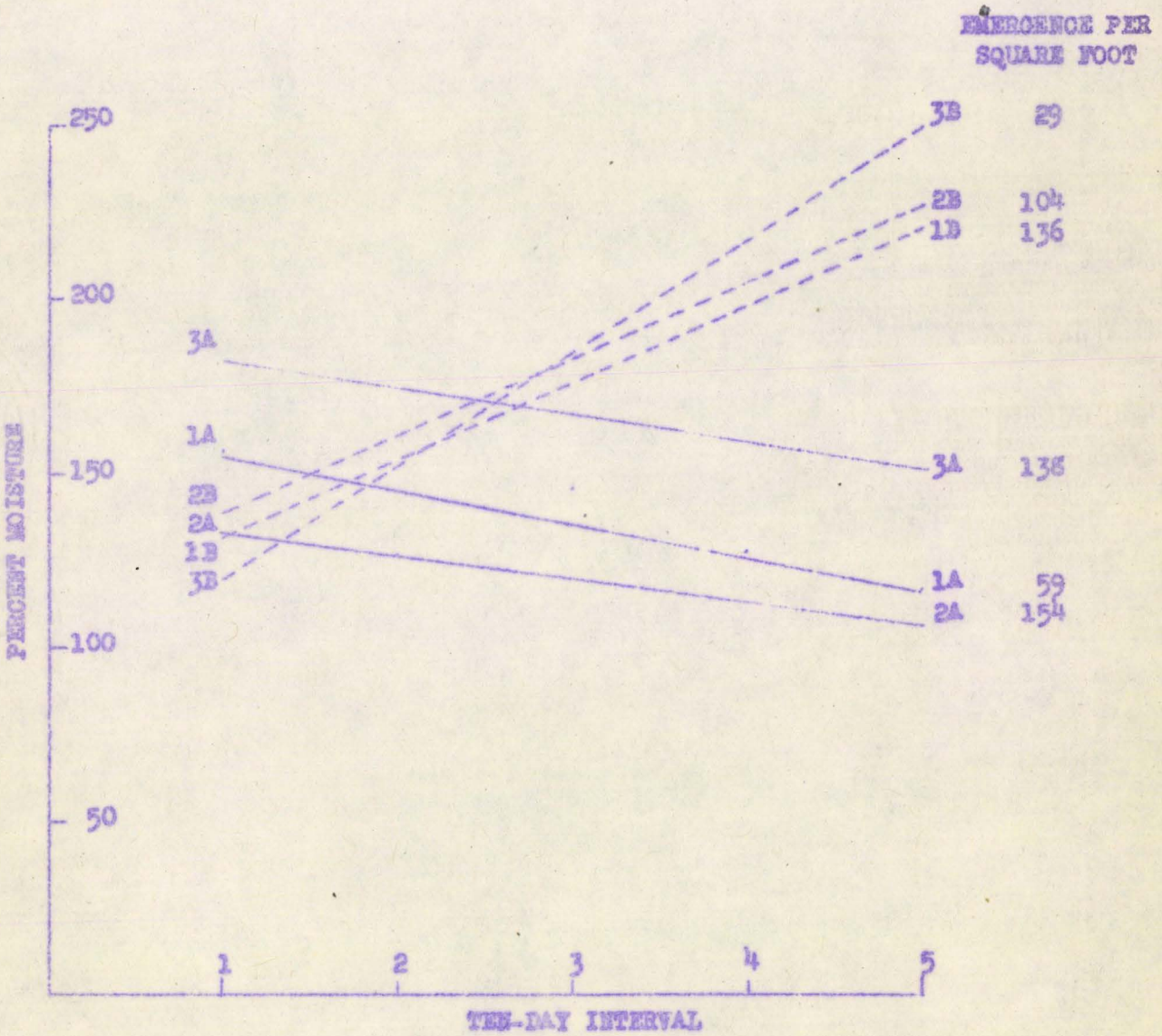

FIGURE 3
PHLOEM MOISTURE TREMDS, SITE I,
IN UNLOPPED AND LOPPED TREES
_____UNLOPPED
- - - - LOPPED

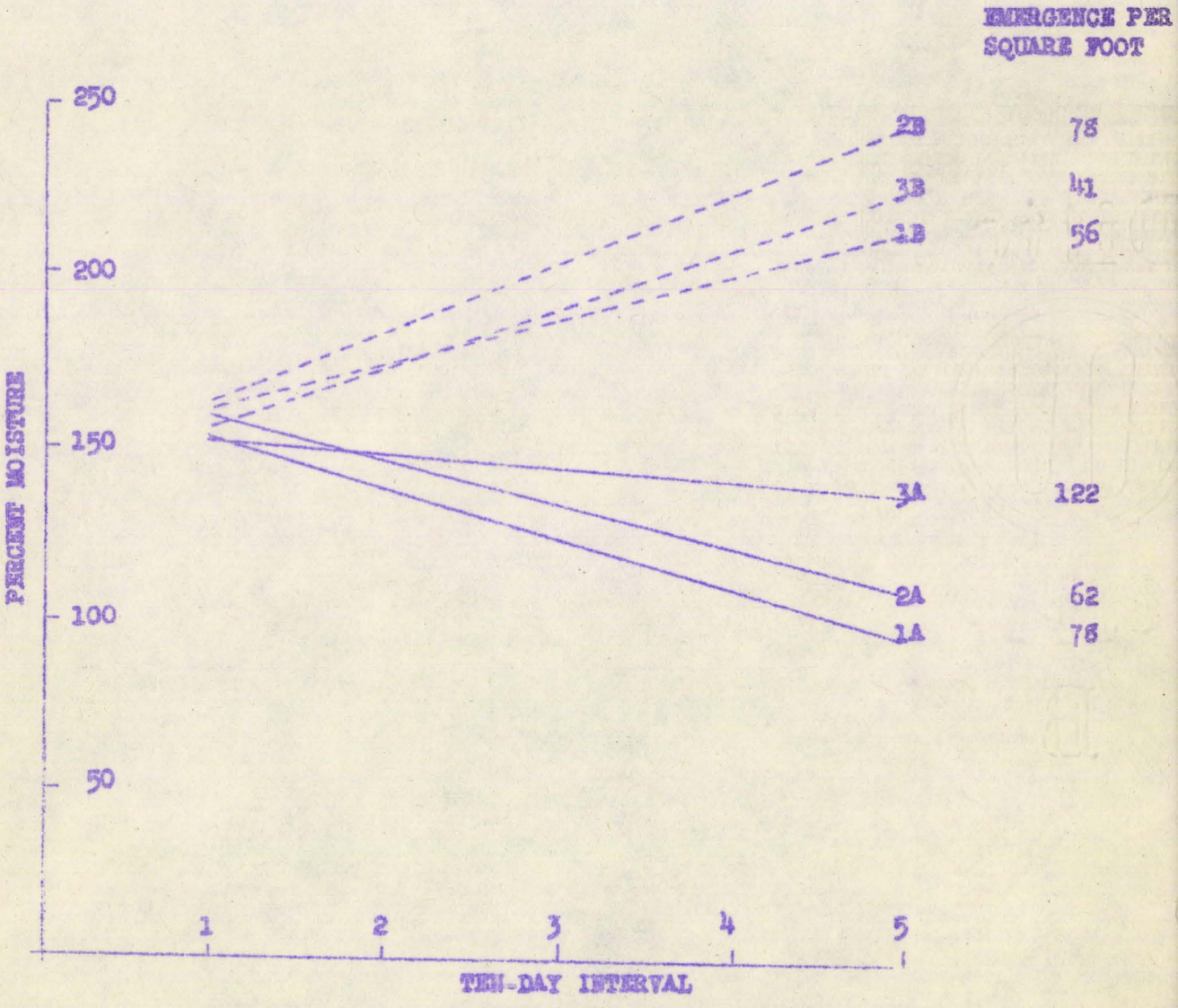

FIGURE 4
SAPWOOD MOISTURE TRENDS, SITE II,
IN LOPPED AND UNLOPPED TREES
_____UNLOPPED
- - - - -LOPPED